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THE BIOLOGY AND ECOLOGY OF THE GIANT FREE EGG CAPSULES OF *ADELOMELON BRASILIANA* LAMARCK, 1811 (GASTROPODA: VOLUTIDAE)

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ABSTRACT

A three-year study was conducted to determine oviposition periods of the volutid gastropod *Adelomelon brasiliana,* the abundance and distribution pattern of its egg capsules in the region of Mar del Plata, Argentina. Results indicate that oviposition was correlated with water temperature. Reproduction occurred from September/October to May/June. Because egg capsules are not attached to the substratum and drift freely on the bottom along a narrow zone close to the shoreline, they can become stranded on the beach after storms, thus suffering mass mortality. This was reflected by a decline in snail recruitment during one study year in which storm surges were frequent and severe. The developmental stages of the egg capsules were characterized, and the proportion of early and late developmental stages determined monthly. This allowed an estimate of recruitment during each reproductive season. Twenty percent of the egg capsules at hatching contained one to three embryos that were considerably smaller than their siblings and 6% of the egg capsules at the same developed stage had one to four teratological embryos. Egg capsules laid down on the sea bottom showed an aggregated distribution pattern. The average developmental time was 57 ± 4 days. Protein and sugar concentration and pH of the intracapsular fluid decreased as embryo development progressed. Several proteins with different molecular weights were present in the intracapsular fluid during the entire intracapsular development.

Key words: *Adelomelon brasiliana*, Volutidae, oviposition, distribution pattern, storm events, intracapsular development stages, reproductive season.

INTRODUCTION

The Family Volutidae is widely distributed being found in the Indo-Pacific Ocean as well as along the coasts of Africa, Antarctica, Central and South America (Poppe & Goto, 1992; Abbott, 1974; Abbott & Dance, 1986).

Recent species belonging to this family undergo intracapsular embryonic development and hatch as crawling juveniles (Penchaszadeh et al., 1999). Volutids from the Indo-Pacific Ocean deposit pineapple-like egg mass containing several egg capsules. In most cases, a single embryo develops within each egg capsule. The egg masses are attached to rocky substrata or to empty bivalve shells, as is the case of species of the genus *Melo* (Allan & Middleton, 1946; Knudsen, 1993; Cotton, 1936).

In volutids from the African Atlantic Ocean of the genus *Cymbium*, egg capsules are brooded in a special "pouch" in the foot, and although egg capsules contain several embryos, only one of these attains complete development (Marche-Marchad, 1968).

South American and Caribbean species differ from those of the African and Indo-Pacific groups in that development occurs within egg capsules containing a variable number of embryos without nutritive nurse eggs, except for *Voluta virescens* Lighfoot, 1786, in which one or two embryos are present at hatching (Bandel, 1976). In general, American egg capsules are almost semi-spherical and are attached to hard substrata by a flat base (Penchaszadeh et al., 1999).

Adelomelon brasiliana, Lamarck, 1811, is a common species in the southwestern Atlantic. It inhabits shallow sandy bottoms from Rio Grande do Sul, Brazil, to San Antonio Oeste, Argentina. Published studies of this species

include its anatomy (Novelli & Novelli, 1982), gonadal cycle (Cledón et al., 2005a), individual growth (Cledón et al., 2005b), and the association with the sea anemone *Antholoba achates* (Drayton, in Dana, 1846) (Luzzatto & Pastorino, 2006).

Egg capsules of *Adelomelon brasiliana* are an exception to the description given above for the South American group because they are laid freely on the sea bottom without being attached to any substratum. This is a unique characteristic among volutid species for which egg capsules have been studied. *Adelomelon brasiliana* egg capsules were first described by d'Orbigny (1846), and the earliest studies on the embryology and the intracapsular liquid were conducted by de Mahieu et al. (1974).

Considering volutids from the Atlantic Ocean, egg capsules are known for the following species: *Zidona dufresnei* (Donovan, 1823), *Odontocymbiola magellanica* (Gmelin, 1791), *Adelomelon beckii* (Broderip, 1836), *Adelomelon ancilla* (Lighfoot, 1786), and *Voluta musica* Linnaeus, 1758 (Penchaszadeh & de Mahieu 1976; Penchaszadeh, 1988; Penchaszadeh et al., 1999; Penchaszadeh & Miloslavich, 2001).

Previous studies on *Adelomelon brasiliana* and *Voluta musica* pointed out an important energetic investment in reproduction, as indicated by the high concentrations of proteins and carbohydrates in the intracapsular liquid, making possible a complete embryonic development within the egg capsule (de Mahieu et al., 1974; Penchaszadeh & Miloslavich, 2001). Such an important investment is also expected for such other volutid species as *Adelomelon ancilla*, *Adelomelon beckii*, *Odontocymbiola magellanica*, and *Zidona dufresnei,* because of their similarity in the reproductive mode (Penchaszadeh et al., 1999).

This study focuses on the embryonic development, developmental time, seasonal oviposition, distribution pattern and intracapsular fluid content of *Adelomelon brasiliana* egg capsules. I also examined the potential effects of inshore drift currents increased by southeast winds, which result in storm surges and unusual swells. All these parameters are relevant in the understanding of this reproductive mode in an environmental context.

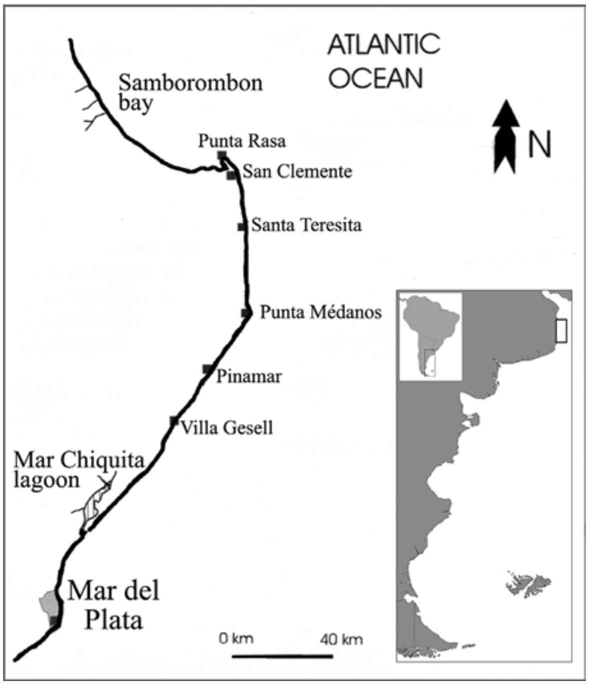

FIG. 1. Geographic position of the sampling area and the most important adjoining localities.

MATERIALS AND METHODS

Samples were taken monthly from April 2000 to March 2003 near the outlet of the Mar del Plata harbor (~38°S) (Fig. 1). Egg capsules were collected with a beam trawl net 1 m wide, 1 cm mesh, along line transects parallel to the shoreline at depths between 8 and 20 m. Each monthly survey consisted of three trawls, which lasted for 15 min each. Taking into account the direction and strength of the current and dominant winds during the trawl operation, the estimated area covered by the net in each event ranged from 900 to 1,500 m^2. Density was expressed as number of egg capsules per 100 m^2.

To determine the distribution pattern of egg capsules on the sea bottom, an additional survey was conducted using the same boat and net as before in 12 randomly chosen sampling sites in the same study area on December 18, 2002. One sample was taken for 10 min at each site. The mean number and SD of all egg capsules obtained from the 12 trawls were calculated.

The external and internal volumes were recorded from 143 egg capsules. The external volume was measured indirectly by the displaced volume using a 500 ml test tube. The intracapsular fluid was extracted and measured with a test tube for the internal volume determinations. A linear regression was performed between the two measures. The volume occupied by the embryos was not considered because in an advanced developmental stage embryos represent less than 5% of the intracapsular volume.

The number and size of embryos per egg capsule were recorded, and the developmental stage of embryos determined following the scale established by de Mahieu et al. (1974). One-way ANOVA was used to determine differences between the number of embryos per egg capsule and their developmental stage. The relationship between the number of embryos and the egg capsule volume was analysed using linear regression.

Mean monthly temperatures of surface water (1 m) and their respective SD were calculated from daily records provided by the Mar del Plata harbor marigraph. The correlation between the mean monthly temperatures of surface water and presence of egg capsules on the sea bottom was made using Kendal's Method (Conover, 1999). This non-parametric statistical method was applied because data did not meet assumptions of normality and homoscedasticity.

During the study period, all storm events taking place in the Partido de la Costa were registered (San Clemente del Tuyú marigraph; López, pers. com.). These were referred to as the number of days with waves exceeding 2.1 m.

The total embryonic developmental time and the developmental time of each stage were determined in aquaria under controlled conditions of salinity (35‰) and temperature (ranging between 18 and 24°C). In the experiment, 30 egg capsules at a very early developmental stage were placed in each of two 200-liter tanks. Seawater was recycled through a refrigerator with an aquarium water pump. Every 2 days, egg capsules were removed from the water for a short period to determine their individual developmental stage (transparency enabled direct scoring) and returned to the aquaria. Aquaria were equipped with a pump for water movement because preliminary experiments had shown that this was a crucial requirement for the viability of embryos in egg capsules at early developmental stage (lower than stage 2).

Recruitment was expressed as the percentage of the number of egg capsules that hatched or were about to hatch (stages 5 to 8), using all egg capsules collected during each reproductive season.

Two ml of intracapsular fluid of 40 egg capsules at different developmental stages were frozen and used for chemical analysis. Protein concentrations were determined using the Lowry method using BSA to build the calibration curve. Total carbohydrate was determined by the Herbert et al. (1971) method. Analytical glucose was used for the calibration curve. After dissecting the living egg capsules, pH was measured at different developmental stages. SDS-page electrophoresis (gels containing 10% acrylamide) was carried out using 3 µg of proteins per lane of the intracapsular fluid previously determined. Biorad prestained standards were used. The gels were stained first with Biorad silver stain plus kit and in a second step with Biorad coomasie blue R-250.

Photographs of embryos between stages 0 and 6 were taken with a digital camera attached to a Zeiss stereoscopic microscope. The shells of embryos at stage 7 were coated with an alloy of gold and palladium and photographed under a Phillips XL-30 scanning electron microscope at 10 x.

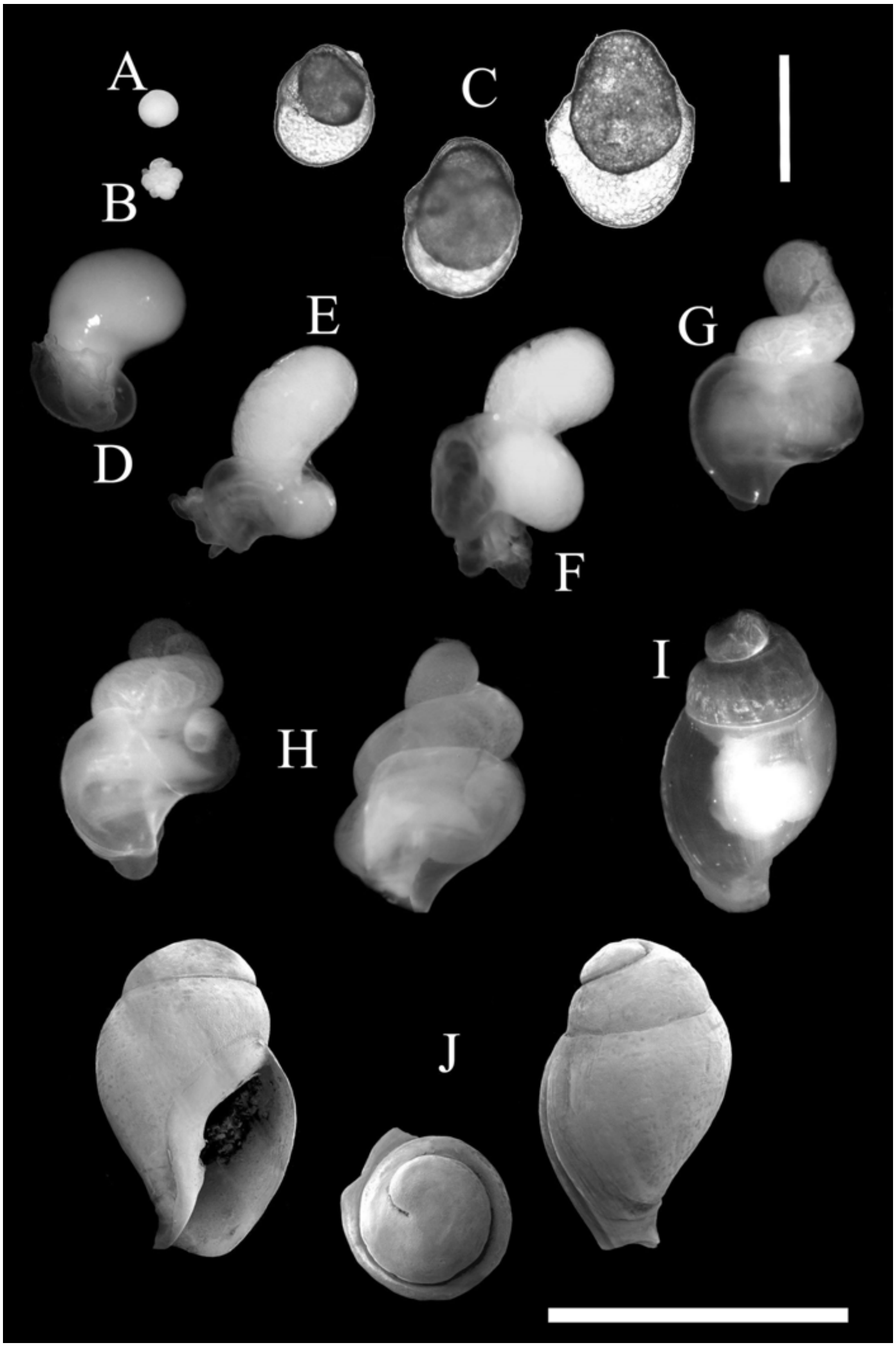

FIG. 2. Embryonic developmental stages of *Adelomelon brasiliana* according to de Mahieu et al. (1974). A: Egg; B: Blastomeres before blastulation; C: Different stages after gastrulation, stage 0; D: Stage 1, Modified veliger; E: Stage 2; F: Stage 3; G: Stage 4; H: Lateral and dorsal views of stage 5; I: Stage 6; J: Apertural, apical and dorsal view of stage 7. Vertical scale = 600 μm, horizontal scale = 1 cm.

RESULTS

Embryonic Development

The unsegmented eggs of *Adelomelon brasiliana* had a small amount of yolk (Fig. 2A), and had a mean diameter of 180 ± 8 µm. They are contained in egg capsules already released to the environment, thus indicating that the entire embryonic development occurred outside the oviduct. Subsequently, embryos undergo a slightly unequal spiral cleavage, in which macromeres do not duplicate the volume of micromers (Fig. 2 B). Development continues until the formation of gastrula. Embryo torsion starts immediately after gastrulation and results in a veliger larva with low movement and a small ciliated velum directing waterflow towards the embryo's mouth. All this developmental process was named stage 0 by de Mahieu et al. (1974) (Fig. 2C). At stage 1 (Fig. 2D), torsion is already completed and retraction of the velum starts. In addition, heart and gills become visible. At stage 2 (Fig. 2E), the second whorl is fully developed, the portion forming the rudiment of the digestive gland, gonads and some other glands can be clearly observed, and the head and foot start to develop. Some of the embryos can be seen crawling on the inner wall of the egg capsule. The rudiment of a translucent layer covering the whole embryo indicates the beginning of shell formation. At stage 3 (Fig. 2F), the embryo keeps growing, the shell is conspicuous, the third whorl starts to develop, and all embryos crawl on the inner wall of the egg capsule. At stage 4 (Fig. 2G), the third whorl is completed and body growth continues. At stage 5 (Fig. 2H), there is a compression of

TABLE 1: Embryonic developmental time, embryo sizes and number of embryos per egg capsule of *Adelomelon brasiliana* at different developmental stages.

Stage of Devel-opment	Time* (in days)	Total length (in mm)	Number of Embryos** (per egg capsule)
0	0	0.180 - 3.500	17.4 ± 4
1	5.5 ± 1.7	3.709 ± 1	15 ± 4.8
2	8.4 ± 2	4.990 ± 1.098	14.8 ± 4.2
3	11.7 ± 2.7	6.272 ± 0.559	14.5 ± 2.6
4	15.6 ± 3.6	6.946 ± 0.749	15.5 ± 3.6
5	21.5 ± 4	8.200 ± 0.437	14.1 ± 3.6
6	31.8 ± 3.6	8.571 ± 0.697	13.9 ± 3.1
7	41.2 ± 4.4	9.704 ± 0.322	15 ± 3.4
8	56.8 ± 4.3	+ 10	

* N (total) = 60
** Main effects ANOVA (p = 0.231, DF = 21, N = 60)

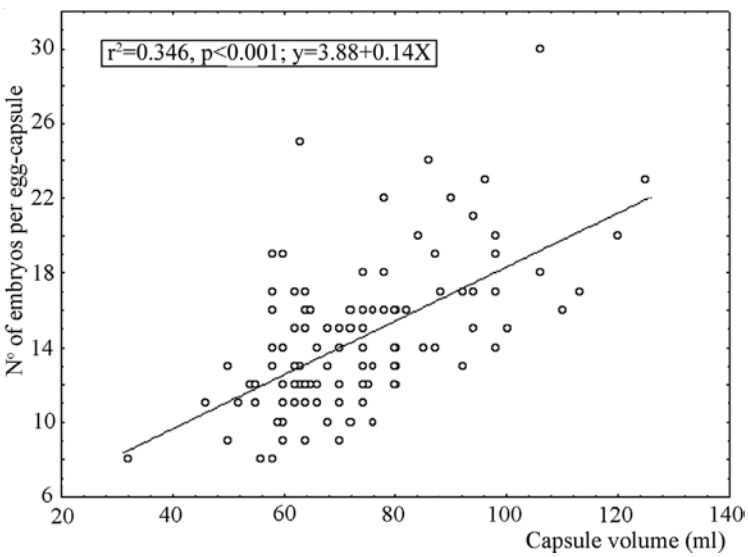

FIG. 3. Distribution of the number of *Adelomelon brasiliana* embryos in relation to egg capsule volume.

early whorls, and shell starts the calcification process. At stage 6 (Fig. 2I), the sutures of all whorls are formed, and calcification increases. These features become more evident at stage 7 (Fig. 2J), when calcification is completed and shell grows to a mean length of 1 ± 0.2 cm until hatching. In this study, hatching is included in stage 8. Embryo sizes at each developmental stage are shown in Table 1.

The number of embryos did not seem to differ among egg capsules at different developmental stages (p = 0.231; Table 1). However, there was a linear relationship between the number of embryos and egg capsule volume (R^2 = 0.3466, p = 0.000; Fig. 3).

Abnormal embryos were recorded (Table 2) in egg capsules at stages 6 and 7 (n = 167). The 20.36% of the egg capsules had 1 to 3 embryos smaller (38 ± 4.5%) than the expected for their developmental stages. These capsules also contained normal embryos. Teratological embryos were also found in 5.98% (n = 10) of the egg capsules. Each egg capsule contained a unique pattern of teratological embryos (Fig. 4). Teratological and normal embryos were found in eight egg capsules, while the other two only contained deformed embryos.

TABLE 2: Percentage of *Adelomelon brasiliana* egg capsules containing different numbers of teratological and underdeveloped embryos, total N = 167.

Number of Embryos	Number of teratological embryos	Number of underdeveloped embryos
1	6	17
2	2	12
3	1	5
4	1	-
Cumulative egg capsules	10	34

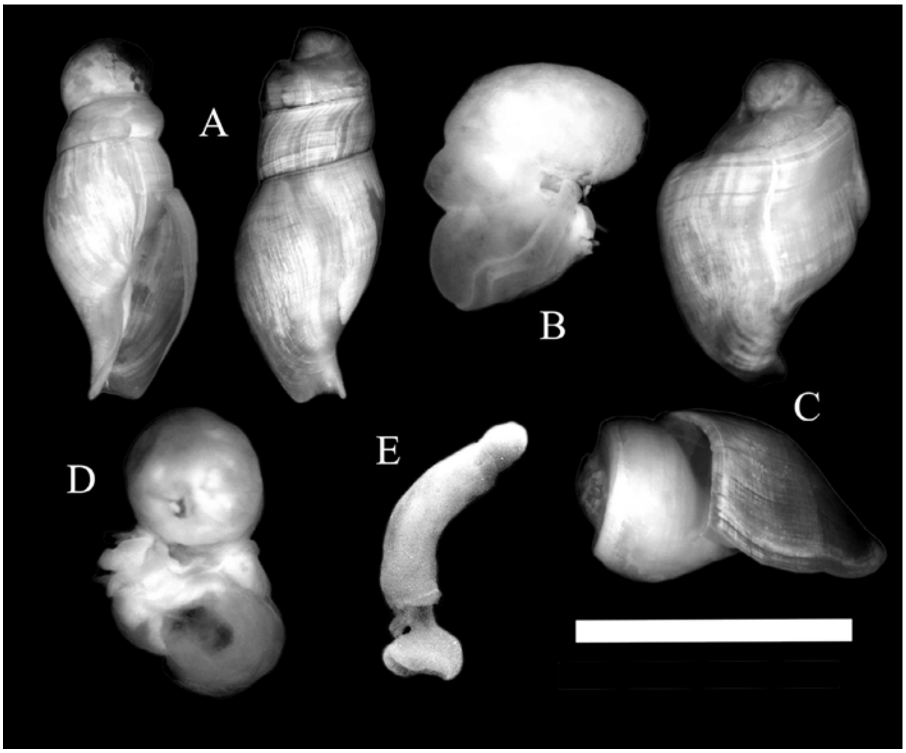

FIG. 4. Teratological embryos at stage 7 of *Adelomelon brasiliana*. A: Apertural and dorsal view of an embryo with enlarged whorls; B: Lateral view of a decalcificated embryo; C: Dorsal and lateral view of an embryo with an overlapped and abnormal growth of the whorls; D: Decalcificated embryo with abnormal growth; E: Decalcificated embryo without whorl formation. Scale bar = 1 cm.

Developmental Time

The developmental time obtained in aquaria was 56.8 ± 4.3 days, and the cumulative developmental time for each stage is detailed in Table 1.

Table 3 shows the total number of captures and the percentages of captures of egg capsules at each developmental stage. The intracapsular embryonic developmental time for each of the three study years could be estimated from this table. During the first study year, capsules in stage 0 were detected on October 28, 2000, and the first hatching egg capsules on January 24, 2001. These data indicate a maximum intracapsular developmental time of 87 days. The same analysis made for the second and third study years showed values of 84 and 98 days, respectively.

TABLE 3: Total captures (N) and percentage of developmental stages of *Adelomelon brasiliana* encapsulated embryos by sampling date.

Date	N	Developmental stage								
		0	1	2	3	4	5	6	7	8
04/27/2000	321	10.2	17.7	15.6	9.3	10.9	9.7	4.9	0.9	20.5
05/24/2000	163	28.2	22.1	11.7	8.6	8.6	4.3	1.2	1.8	13.5
06/23/2000	32	-	3.1	-	3.1	21.9	12.5	6.3	9.4	43.8
07/26/2000	49	-	-	-	-	-	-	2	-	98
08/28/2000	-	-	-	-	-	-	-	-	-	-
09/25/2000	-	-	-	-	-	-	-	-	-	-
10/28/2000	23	100	-	-	-	-	-	-	-	-
11/28/2000	69	94.2	1.5	1.4	2.9	-	-	-	-	-
12/14/2000	31	10	25.8	16.1	19.4	6.5	3.2	-	-	-
01/24/2001	52	5.8	3.8	3.8	3.8	7.7	5.8	15.4	5.8	48.1
02/20/2001	620	0.5	0.8	0.2	0.5	0.3	0.3	0.3	1.9	95.2
03/20/2001	11	9.1	36.4	-	9.1	-	-	-	9.1	36.4
04/23/2001	12	8.1	33.3	-	8.3	-	-	8.3	8.3	33.3
05//04/2001	27	59.3	-	-	-	3.7	-	3.7	-	33.3
05/24/2001	43	9.3	-	2.3	4.7	4.7	7	4.7	20.9	46.5
06/23/2001	12	-	-	-	-	-	-	-	-	100
07/26/2001	-	-	-	-	-	-	-	-	-	-
08/25/2001	-	-	-	-	-	-	-	-	-	-
09/10/2001	15	100	-	-	-	-	-	-	-	-
09/20/2001	-	-	-	-	-	-	-	-	-	-
10/20/2001	9	66.7	11.1	-	22.2	-	-	-	-	-
10/28/2001	20	100	-	-	-	-	-	-	-	-
12/04/2001	24	87.5	-	4.2	-	-	-	-	-	8.3
12/27/2001	110	32.7	30	20.9	8.2	6.4	-	-	1.8	-
01/29/2002	71	19.7	14.1	7	4.2	1.4	-	-	16.9	36.6
02/20/2002	13	69.2	30.8	-	-	-	-	-	-	-
02/26/2002	22	50	4.5	4.5	-	36.4	-	-	4.5	-
03/25/2002	62	14.5	3.2	14.5	17.7	9.7	16.1	4.8	17.7	1.6
04/20/2002	31	51.6	9.7	-	3.2	-	3.2	3.2	6.5	22.6
05/30/2002	20	60	15	-	5	-	5	-	-	15
06/31/2002	-	-	-	-	-	-	-	-	-	-
07/25/2002	-	-	-	-	-	-	-	-	-	-
08/27/2002	-	-	-	-	-	-	-	-	-	-
09/30/2002	70	100	-	-	-	-	-	-	-	-
11/08/2002	65	100	-	-	-	-	-	-	-	-
12/05/2002	222	77.5	10.8	10.8	1	-	-	-	-	-
01/08/2003	16	50	18.8	-	-	-	-	-	-	31.2
02/06/2003	116	41.38	4.3	2.6	3.4	3.4	5.2	3.4	1.7	32.8

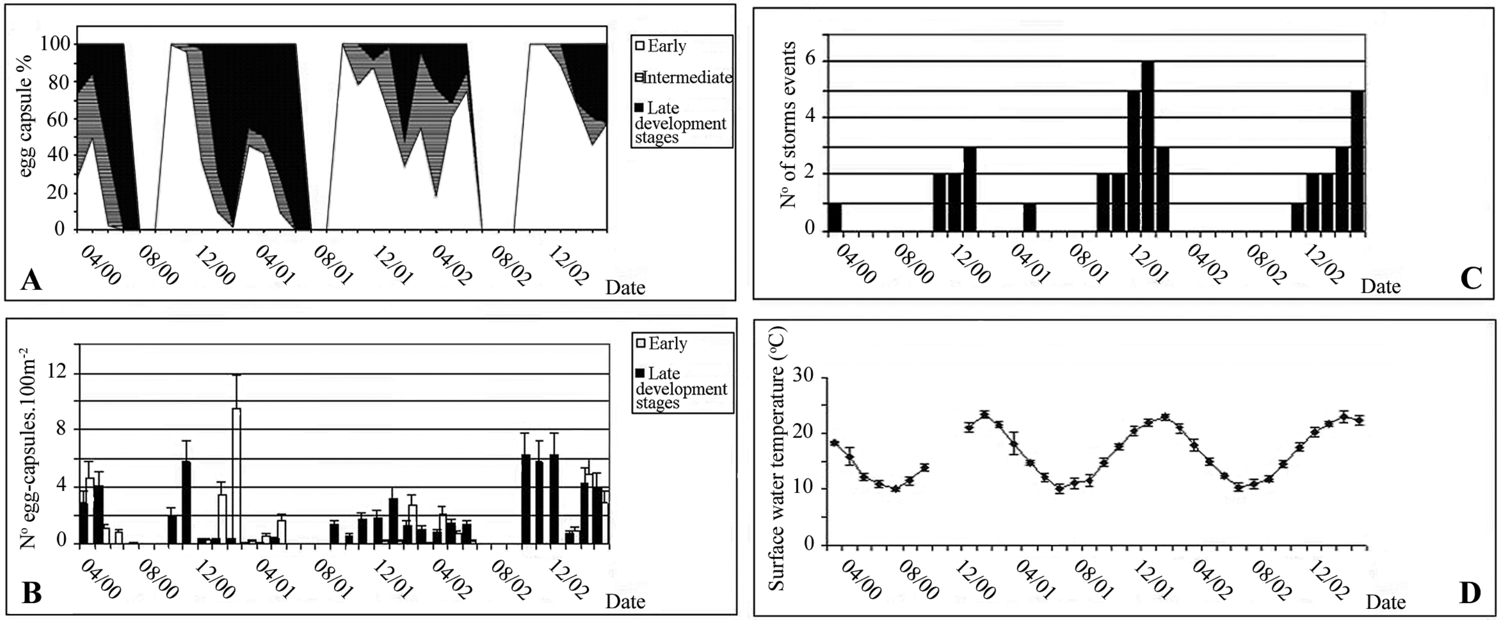

FIG. 5. A: Mean percentage distribution of encapsulated embryos stages; B: Total egg capsule densities; C: Storms surges events (San Clemente del Tuyú marigraph); D: Mean water surface temperatures (Mar del Plata marigraph).

FIG. 6. Egg capsules of *Adelomelon brasiliana* stranded on a typical beach in Buenos Aires Province after storm surges events. Photograph by Ana Fazio.

Areal Abundance and Distribution Pattern over Time

Reproduction had a seasonal pattern, and egg capsules were absent during the coldest winter months. There was a correlation between mean water temperatures (Fig. 5D) and presence/absence of early developmental stages egg capsules on the sea bottom (τ =0.56, n = 34) (Figs. 5A, B).

The maximum density of egg capsules during the entire study period, regardless their developmental stage, was 30/100 m^2 in March 2000.

Egg capsules were found stranded in high densities on the emerged beach with no possibility of returning to the sea after a long period of storm surges characterized above (Fig. 6).

Recruitment was related to storm events recorded seasonally during the study period. Figures 5A and B, show a decrease in recruitment during summer 2001–2002, when surge storms were frequent and intense (Fig. 5C). In this period, recruitment was approximately 40%, whereas it was 95% for the summer 2000–2001 period.

The mean density of egg capsules collected to determine their distribution pattern was 3.55 ± 5.65 egg capsules/100 m^2, suggesting an aggregated distribution as they drift freely with littoral currents.

Biochemical Content of the Intracapsular Fluid

Protein (Fig. 7A) and carbohydrate (Fig. 7B) concentration and pH (Fig. 7C) decreased during embryo development (R^2 = 0.64, 0.47 and 0.7 respectively). The dissected capsules had a gelatinous substance on its internal face only present in the earliest developmental stages (up to stage 2). Several proteins with different molecular weights were present in the intracapsular fluid (Fig. 7D) without evident variation in composition throughout intracapsular development.

The regression between external (*ev*) and internal volume (*iv*) is significant (p = 0.000, R^2 = 0.979) and the linear equation is: $iv = 0.89\ ev$. The mean internal volume (*mv*) was 72.1 ± 14.9 ml.

The available protein per embryo in the intracapsular fluid during the embryo development (*Ped*) (Fig. 8A) was $Ped = PC_{st}\ X\ mv / en_{st}$ where PC_{st} is the total protein per developmental stage shown in Fig. 7A and en_{st} is the media number of embryos per developmental stage (Table 1).

The available carbohydrate per embryo in the intracapsular fluid during development (*Ced*) (Fig. 8A) was: $Ced = HC_{st}\ X\ mv / en_{st}$ where HC_{st} is the total carbohydrate per developmental stage shown in figure 7B. During the earliest developmental stages (0–2) the *Ped* and *Ced* remained constant, decreasing as the development progressed (Fig. 8).

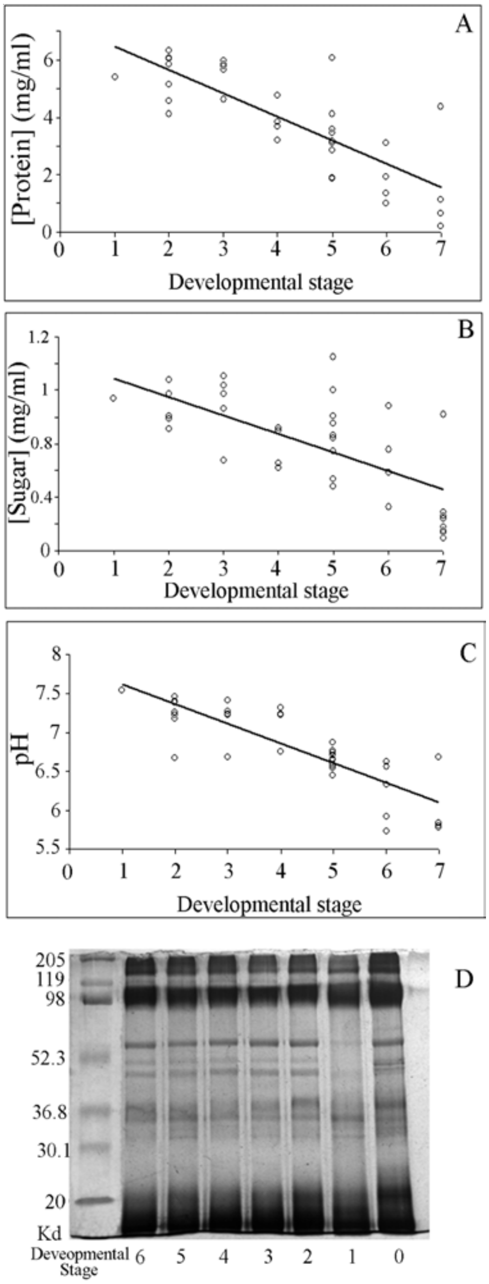

FIG. 7. Different developmental stages of *Adelomelon brasiliana*. A: Protein concentration; B: Sugar concentration; C: PH; D. SDS-page.

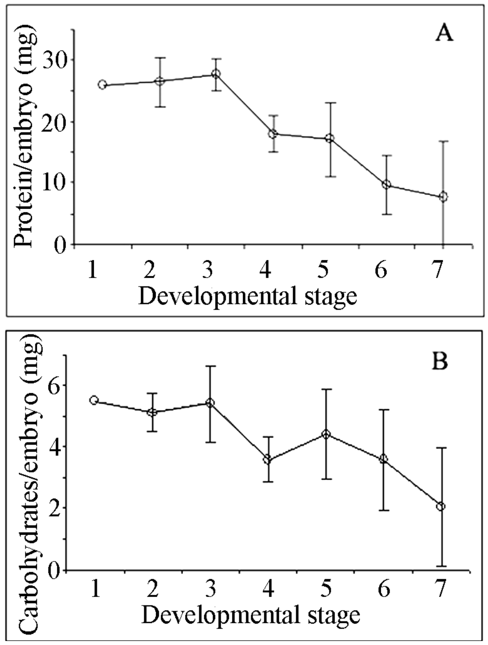

FIG. 8. Available total proteins (A) and carbohydrates (B) per embryo in the intracapsular fluid at the different developmental stages.

DISCUSSION

The small amount of yolk in uncleaved eggs of *Adelomelon brasiliana* may be related to their intracapsular development, since the intracapsular fluid contains the largest source of food available for embryonic development (de Mahieu et al., 1974). This makes possible the first cleavage of blastomeres without remarkable differences in size between macromeres and micromeres. The veliger stage of *Adelomelon brasiliana* has a very small ciliated velum providing little movement, in contrast to that of other volutid species. For example, the veliger intracapsular stage of *Voluta musica* possesses a large velum and considerable self-movement (Penchaszadeh & Miloslavich, 2001). This suggests that in *A. brasiliana*, the velum may exclusively have a feeding function at early developmental stages. The small velum disappears after stage 1, and embryos crawl on the inner wall

of the egg capsule. Except for the veliger stage, no other remarkable differences in embryonic development are observed between *A. brasiliana* and the rest of the volutid species studied.

The difference between the numbers of embryos per capsule among developmental stages is not significant, although a tendency to decrease in number can be observed (Table 1). The presence of some underdeveloped or teratological embryos (Fig. 4, Table 2) could be a response of competition between developing embryos or a contamination effect, because high levels of tributyltin antifouling paint compounds (TBTs) were found inside *A. brasiliana* egg capsules (Goldberg et al., 2004) in the same study area. This could be related to the variability of embryos number not explained by egg capsule volume (Fig. 3).

The oviposition process of *A. brasiliana* is still unknown. The mean volume of egg- capsules recorded in this study was 80 ml (Fig. 2), corresponding to 9 cm in height and 7 cm in width approximately. The oviduct and vaginal opening of *A. brasiliana* are similar to those of other snail species with similar shell length (Novelli & Novelli, 1982). Although direct observation is needed to understand how the oviposition process is undertaken, these data suggest that the egg capsule of *A. brasiliana* is a loose structure, attaining its oval shape and ultimate hardness once laid down in contact with water.

González & Ibarra (2001) postulated that the climate in the study area is undergoing an effect known as "tropicalization", which results in the concentration of rainfall during summer, together with the frequent co-occurrence of southeastern winds. According to the authors, the "tropicalization" effect shows an increasing intensity and frequency at least since the decade of 1960 when their study began. This phenomenon brings storm surges to the coastal area, leading to the stranding of invertebrates on the beach, as is the case for *A. brasiliana* egg capsules. A large number of these were found along the coast (Fig. 6), where they are subject to mass-mortality by sea-bird predation or desiccation (Penchaszadeh et al., 2000). The proportion of egg capsules at early and late developmental stages was similar during the summer period 2000–2001, whereas there was a larger proportion of egg capsules at early developmental stages in summer 2001–2002, thus indicating lower recruitment. Likewise, total abundance of egg capsules during the second study year was lower than in the first year. These results are related to the frequency and intensity of storm surges, since storm events were fewer and lasted for a shorter time in the first period than in the second (Fig. 5).

The experimental results indicate that the total developmental time of *A. brasiliana* was two months, in contrast to three months as reported by de Mahieu et al., (1974). This difference is possibly due to the methodology used, since these authors made four consecutive samplings over one reproductive season. Using the same analysis for data from the three reproductive seasons, I found that *Adelomelon brasiliana* took 87, 84, and 98 days, respectively, to complete the intracapsular development (Table 3). The values given above are possible overstimated by the monthly nature of samplings.

As in the present work, de Mahieu et al. (1974) analysed the nourishing substances in the intracapsular liquid. Penchaszadeh & Miloslavich (2001), based on that work, pointed out that the egg capsules of *A. brasiliana* have the highest amount of proteins per embryo in the intracapsular liquid among the volutid species and other families analyzed (i.e., Muricidae, Buccinidae, Melongenidae, and Marginellidae). Although information provided by de Mahieu et al. (1974) described considerably larger quantities of proteins than reported here, both results came to the conclusions referred above. There is a high-energy allocation for embryos developing in egg capsules drifting in sea currents and exposed to the risks mentioned above. However, the results can be explained in terms of availability and abundance of food resources in the environment, which is characterized by a high productivity due to fluvial processes of the Rio de la Plata estuary. In addition, *A. brasiliana* would have high reproductive effort without an insurance of its recruitment, probably due to the lack of competitors, been a carnivorous at a high trophic level.

The decrease in the total proteins and carbohydrates per embryo after stage 3 shown in Fig. 8 could be a result of a change in the food source for the embryos. During the earliest stages of development, the gelatinous layer found in the inner wall could be maintained by the protein and carbohydrates concentration of the intracapsular fluid media.

After stage 2, when the embryos change from "swimming" in the intracapsular fluid media to crawling on the inner face of the egg capsule, this capsule itself could become a source of food for the embryos that crawl and probably feed on it.

The descending intracapsular pH during embryo development was also detected by de Mahieu et al. (1974). In the present work, I found greater differences between intracapsular pH of earliest and latest developmental stages. Despite the differences recorded, we both agree that the acidification of the internal media of the egg capsule occurs. The egg capsule wall permeability is limited, since it maintains an ionic internal media different from the surrounding environment. The pH could be also limiting the time that the embryos could survive in the sealed egg capsule at values lower than 6 in latest developmental stages.

Free egg capsules in *A. brasiliana* could be interpreted as a strategy for instantaneous dispersal. Other volutid species such as *Zidona dufresnei*, *Adelomelon beckii* or *Adelomelon ancilla* that have a different reproductive mode by attaching their egg capsules to the substratum (Penchaszadeh et al., 1999; Ayçaguer, 2002), show a similar or wider geographic distribution than that of *A. brasiliana*. The free egg capsules of *A. brasiliana* may represent an adaptation to the environment, since this species inhabits sandy bottoms with almost no suitable substratum for egg capsule attachment.

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